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Sikora, Martin; Seguin-Orlando, Andaine; Sousa, Vitor C.; Albrechtsen, Anders; Korneliussen, Thorfinn Sand; Ko, Amy; Rasmussen, Simon; Dupanloup, Isabelle; Nigst, Philip R.; Bosch, Marijolein D.; Renaud, Gabriel; Allentoft, Morten Erik; Margaryan, Ashot; Vasilyev, Sergey V.; Veselovskaya, Elizaveta V.; Borutskaya, Svetlana B.; Deviese, Thibaut; Comeskey, Dan; Higham, Tom; Manica, Andrea; Foley, Robert; Meltzer, David J.; Nielsen, Rasmus; Excoffler, Laurent; Lahr, Marta Mirazon; Orlando, Ludovic Antoine Alexandre; Willerslev, Eske

Published in:
Science

DOI:
[10.1126/science.aao1807](https://doi.org/10.1126/science.aao1807)

Publication date:
2017

Document version
Publisher's PDF, also known as Version of record

Citation for published version (APA):
Sikora, M., Seguin-Orlando, A., Sousa, V. C., Albrechtsen, A., Korneliussen, T. S., Ko, A., Rasmussen, S., Dupanloup, I., Nigst, P. R., Bosch, M. D., Renaud, G., Allentoft, M. E., Margaryan, A., Vasilyev, S. V., Veselovskaya, E. V., Borutskaya, S. B., Deviese, T., Comeskey, D., Higham, T., ... Willerslev, E. (2017). Ancient genomes show social and reproductive behavior of early Upper Paleolithic foragers. *Science*, 358(6363), 659-662. <https://doi.org/10.1126/science.aao1807>

HUMAN EVOLUTION

Ancient genomes show social and reproductive behavior of early Upper Paleolithic foragers

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Present-day hunter-gatherers (HGs) live in multilevel social groups essential to sustain a population structure characterized by limited levels of within-band relatedness and inbreeding. When these wider social networks evolved among HGs is unknown. To investigate whether the contemporary HG strategy was already present in the Upper Paleolithic, we used complete genome sequences from Sunghir, a site dated to ~34,000 years before the present, containing multiple anatomically modern human individuals. We show that individuals at Sunghir derive from a population of small effective size, with limited kinship and levels of inbreeding similar to HG populations. Our findings suggest that Upper Paleolithic social organization was similar to that of living HGs, with limited relatedness within residential groups embedded in a larger mating network.

Opportunities to investigate the population dynamics of early anatomically modern human (AMH) populations are rare owing to a dearth of human remains, with wide variations in ancient population size estimates from ethnographic and archaeological data (1, 2). In the absence of evidence for true contemporaneity among individuals recovered archaeologically, the population structure of foraging groups is even harder to establish. Exceptions are cases of multiple Upper Paleolithic individuals buried simultaneously or originating from sufficiently close temporal and spatial proximity that they may represent a single social group.

One such example of multiple burials is Sunghir, a site harboring two of the most extraordinary Upper Paleolithic burials known (3, 4) (figs. S1 and S2 and tables S1 to S4): one of an adult male [Sunghir 1 (SI)] and another of two sub-adults [Sunghir 2 and 3 (SII and SIII)], originally thought to be a boy and girl, interred head-to-head. All remains were covered in ochre and were accompanied by rich grave goods including ivory beads and spears, armbands, and carvings, as well as arctic fox canines. Adjacent to SII was the fem-

oral diaphysis of an adult [Sunghir 4 (SIV)] that had been polished, hollowed out, and filled with red ochre. The site also yielded other less complete human remains, some of uncertain stratigraphic provenance [Sunghir 5 to 9 (SV to SIX)]. Radiocarbon analyses place the age of SI to SIV between 33,600 and 34,600 years (5, 6). The homogeneity in morphological traits (e.g., metopism) among the remains, as well as signs of possible congenital pathologies in SIII, have been interpreted as evidence of inbreeding (3). Other Upper Paleolithic individuals with reported congenital or degenerative pathologies (e.g., at Barma Grande and Dolní Věstonice) (3) reinforce the view that Upper Paleolithic groups were small and susceptible to inbreeding, possibly as extensive as what has been reported for the Altai Neandertal (7). However, genomic data available for some of those individuals (8) were of insufficient coverage to infer population sizes or inbreeding levels.

We screened six of the Sunghir individuals (SI to SVI) to assess DNA preservation; five of them (all but SV) yielded sufficient endogenous DNA for genome sequencing. We sequenced these genomes to an average depth of coverage ranging

from 1.11× to 10.75× (figs. S3 and S4 and tables S5 and S6) and compared them to panels of modern and ancient human genomes (4). All individuals were genetically male on the basis of the fraction of Y chromosome reads (table S7), including SIII, who was previously identified as female (3). Contamination levels from X chromosome heterozygosity were low (0.33 to 0.90%; table S5), except for SVI (13.1%). Radiocarbon dates indicate that whereas SV is only slightly more recent than the other individuals, SVI is from ~900 years before the present (figs. S5 and S6 and tables S8 to S10). Together with mitochondrial DNA (mtDNA) and Y chromosome haplogroups (W3a1 and I2a1b2, respectively), these data indicate that SVI is not associated with the Upper Paleolithic burials at the site; SVI was therefore excluded from further analyses.

Analyses of mtDNA genomes place SI to SIV in haplogroup U, consistent with West Eurasian and Siberian Paleolithic and Mesolithic genomes (9) (fig. S7 and table S5). SI belongs to haplogroup U8c; the sequences for the three individuals from the double burial (SII to SIV) are identical and belong to haplogroup U2, which is closely related to the Upper Paleolithic Kostenki 12 (8) and Kostenki 14 (10) individuals. Phylogenetic analyses of the Y chromosome sequences place all Sunghir individuals in an early divergent lineage of haplogroup C1a2 (fig. S8 and tables S12 to S15). Y chromosome haplogroup C1, which is rare among contemporary Eurasians, has been found in other early European individuals, including the ~36,000-year-old Kostenki 14 (11).

We investigated the degree of relatedness among the Sunghir individuals with a method that allows relationship inferences up to the third degree but does not rely on allele frequencies (4). Surprisingly, none of them were found to be closely related (that is, third degree or closer), even though the SII to SIV individuals buried together share both mitochondrial and Y chromosome lineages (Fig. 1 and tables S16 to S23). We then inferred genomic segments that were identical by descent (IBD) and homozygous by descent (HBD) from three higher-coverage Sunghir genomes (SII to SIV) and a panel of ancient and contemporary humans (4). We compared their distributions to those inferred from whole genomes obtained using coalescent simulations (12) of randomly mating populations with varying effective population sizes (N_E) (fig. S9). The distributions of HBD tracts were different between AMHs and archaic humans, indicating small effective population sizes and/or recent inbreeding in archaic

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Fig. 1. Relatedness among ancient Eurasians. Kinship coefficients and R1 ratios (4) were inferred from IBS counts. **(A)** Pairs of Upper Paleolithic individuals, using 1000 Genomes Phase 3 single-nucleotide polymorphism (SNP) sites. **(B)** Pairs of ancient Eurasians, using 1240K capture SNP sites. Within-group pairs of Sunghir are highlighted.

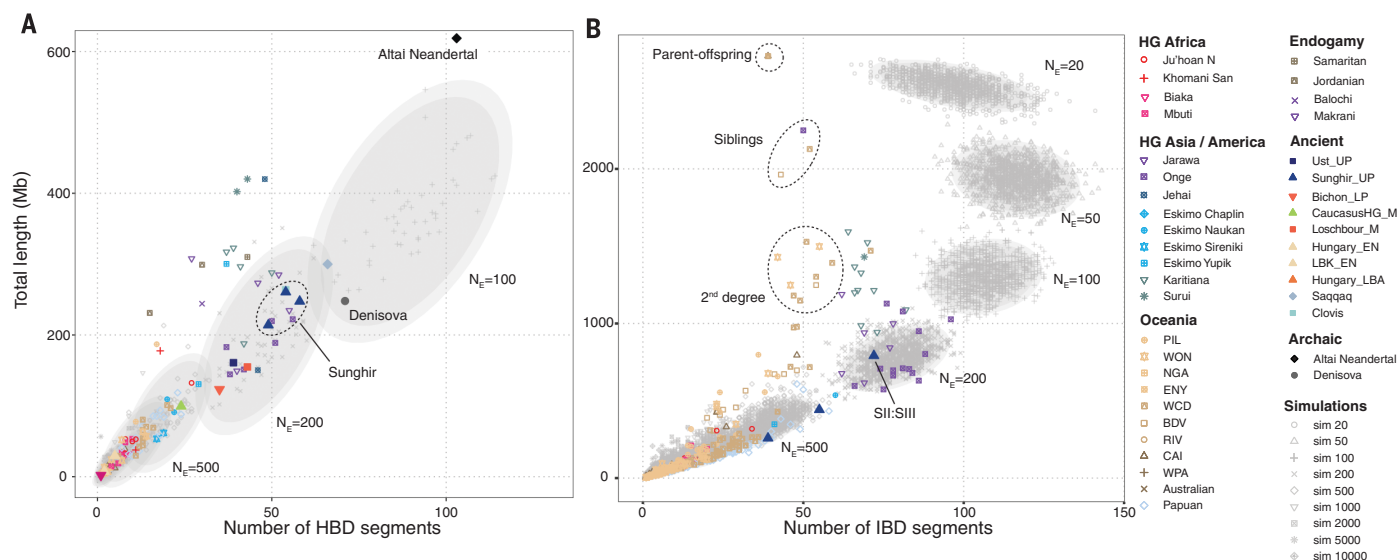
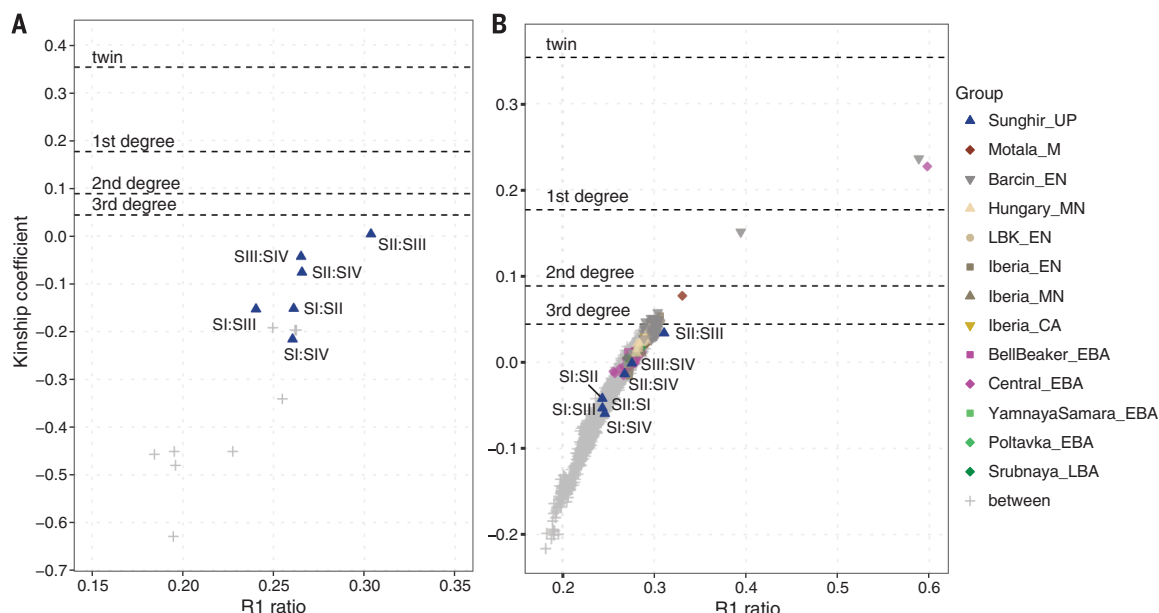


Fig. 2. Identity by descent and recent effective population sizes. **(A and B)** Distributions of the number and total length of HBD and IBD segments in modern, ancient, and archaic humans (Altai Neandertal and Denisovan). Ellipses indicate 95th percentile (dark gray) and 99th percentile (light gray) of the distributions inferred from simulated data of various N_E values. Individuals with previously described close relatedness and their degree are indicated in (B). **(C)** Distributions of inferred recent effective population sizes for modern and ancient HGs with a minimum of three individuals, as well as simulated data sets of randomly mating populations with a range of N_E values. For each population, a pair of symbols and box plots indicates the distributions of population sizes inferred from individual HBD (left) and pairwise IBD tracts (right).

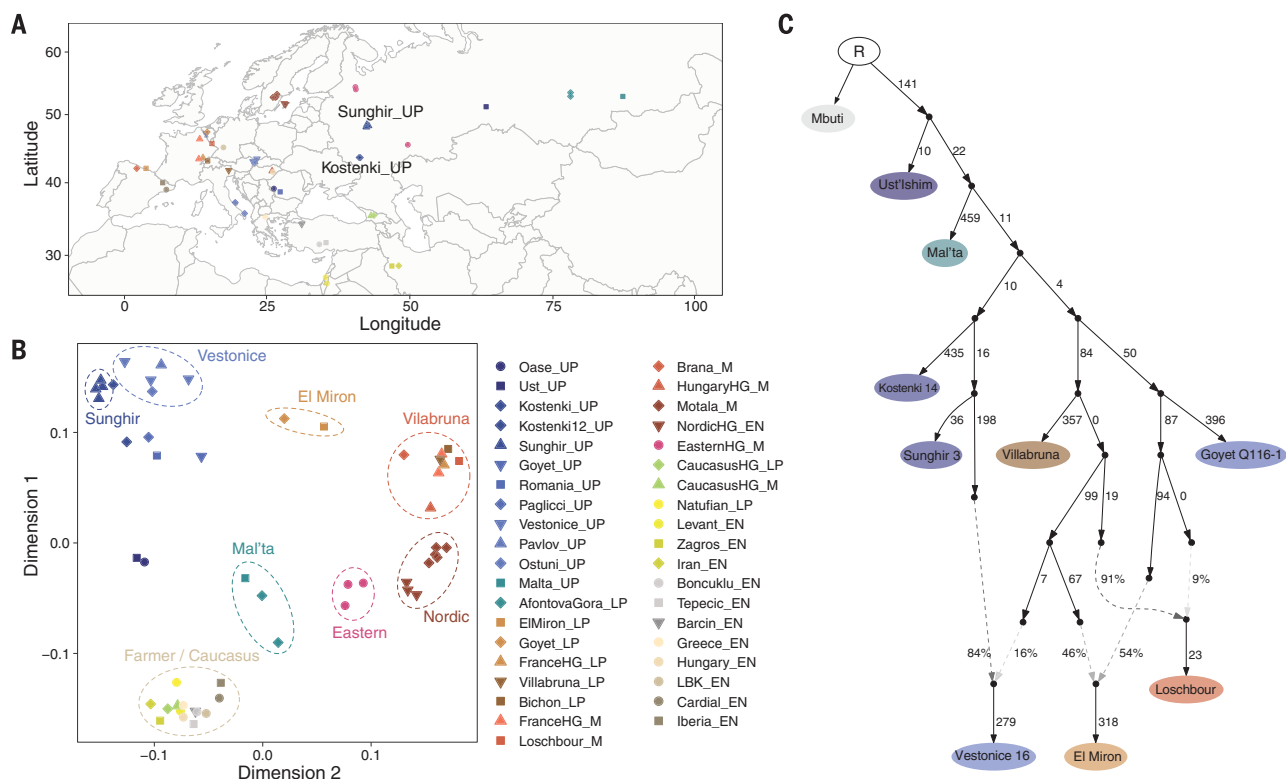


Fig. 3. Genetic affinities of the Sunghir individuals. (A) Geographic locations of ancient Eurasian individuals used in the analysis. **(B)** Multidimensional scaling of ancient individuals based on pairwise

shared genetic drift [outgroup- f_3 statistics $f_3(\text{Mbuti}; \text{Ancient}_1, \text{Ancient}_2)$]. **(C)** Admixture graph showing the best fit of Sunghir with other early Eurasians.

individuals, particularly the Altai Neandertal (7, 13) (Fig. 2A and figs. S10 to S14).

Patterns of pairwise IBD sharing successfully detect close genetic relatives in modern individuals (Fig. 2B). However, the Sunghir pairs do not share sufficiently long IBD tracts to suggest relatedness at the first or second degree, consistent with the results from genome-wide identity-by-state (IBS) counts (Fig. 2B and fig. S15). Interestingly, the effective population sizes tended to be higher ($N_E \sim 500$) for two of three Sunghir pairs than those estimated from HBD segments ($N_E \sim 200$). N_E from both HBD and IBD tracts (4) was within the range of, or slightly higher than, that of contemporary non-African HG populations (Fig. 2C), particularly from genetically isolated groups (14).

Genetic clustering of ancient individuals using outgroup- f_3 statistics $f_3(\text{Mbuti}; \text{Ancient}_i, \text{Ancient}_j)$ indicates shared genetic drift and tight clustering of the Sunghir individuals, which form a clade to the exclusion of all other individuals (Fig. 3, figs. S16 to S20, and tables S28 and S29). Furthermore, we find genetic affinities between the Sunghir individuals and those from Kostenki (12 and 14), as well as with the “Věstonice cluster” (8) associated with the Upper Paleolithic Gravettian culture.

Individuals mapped onto a previously inferred admixture graph of early Eurasians (4, 8) placed the Sunghir cluster as a descendent of a lineage related to the Kostenki 14 individual, contributing the major fraction of the ancestry of the Věstonice cluster (Fig. 3C and figs. S21 to S24). Adding the

low-coverage Kostenki 12 individual suggests a closer relationship with the Sunghir group rather than with the earlier Kostenki 14 individual (fig. S25). Kostenki 14 shows substantial population-specific drift after its divergence from the shared ancestor with Sunghir, allowing us to reject a direct ancestral relationship to both Sunghir and Kostenki 12 (fig. S26). These results suggest that the people at Kostenki were at least partially replaced by later groups related to Sunghir, which exhibit genetic affinities with individuals of the Gravettian culture, which extended to Western Europe.

Our high-coverage Sunghir individual (SIII) allows us to explore quantitative models of Eurasian demographic history. Using coalescent-based modeling of the site frequency spectrum (fig. S27), we estimate that SIII diverged ~38,000 years ago [95% confidence interval (CI), 35,000 to 43,000] from the lineage ancestral to contemporary Europeans, with a relatively small effective population size ($N_E = 297$; 95% CI, 158 to 901) (Fig. 4A, figs. S28 and S29, and tables S24 and S25). The Ust'-Ishim genome, a 45,000-year-old Upper Paleolithic individual from Siberia (I5) who diverged from the Asian lineage ~48,000 years ago (95% CI, 45,000 to 55,000) soon after the initial divergence among Eurasians ~52,500 years ago (95% CI, 49,000 to 57,000), indicates a comparably higher effective population size ($N_E = 1203$; 95% CI, 253 to 7098) (Fig. 4B, figs. S30 and S31, and tables S26 and S27). The best-fit models also suggest a common Neanderthal admixture event shared by all Eurasians 55,000 years ago (95% CI, 52,000 to 63,000), con-

sistent with previous estimates (11, 15). However, we also find evidence of multiple Neandertal admixture events in both SIII (36,000 years old; 95% CI, 34,000 to 42,000) and Ust'-Ishim (47,000 years old; 95% CI, 44,000 to 51,000), the latter introgression providing an estimated 0.6% (95% CI, 0.002 to 1.53) of Neandertal ancestry to SIII. That excess may reflect either (i) further pulses of Neandertal introgression, or (ii) selection against Neandertal introgressed regions in AMHs, as previously suggested (8, 16–18). Analysis of putative archaic-introgressed genomic segments (4) confirms a higher level of Neandertal ancestry and a longer average Neandertal segment length among Upper Paleolithic individuals, in agreement with their closer proximity to the human-Neandertal admixture event than present-day Eurasians (fig. S36). Assuming that the Sungir individuals are contemporaneous (4), we obtain a refined estimate of the time since admixture at 770 generations (95% CI, 755 to 786). Accounting for the uncertainty of both the admixture estimate and ^{14}C ages, this corresponds to an admixture date between the ancestors of Sungir and Neandertals between 53,600 and 58,100 years ago [assuming 29 years per generation (19)], in agreement with the results obtained from coalescent modeling (fig. S37).

Our results suggest a social and population network of HG demes that preferentially mated within subgroups, with exogamy and regular exchanges between demes. Among contemporary HGs, primary kin constitute <10% of residential

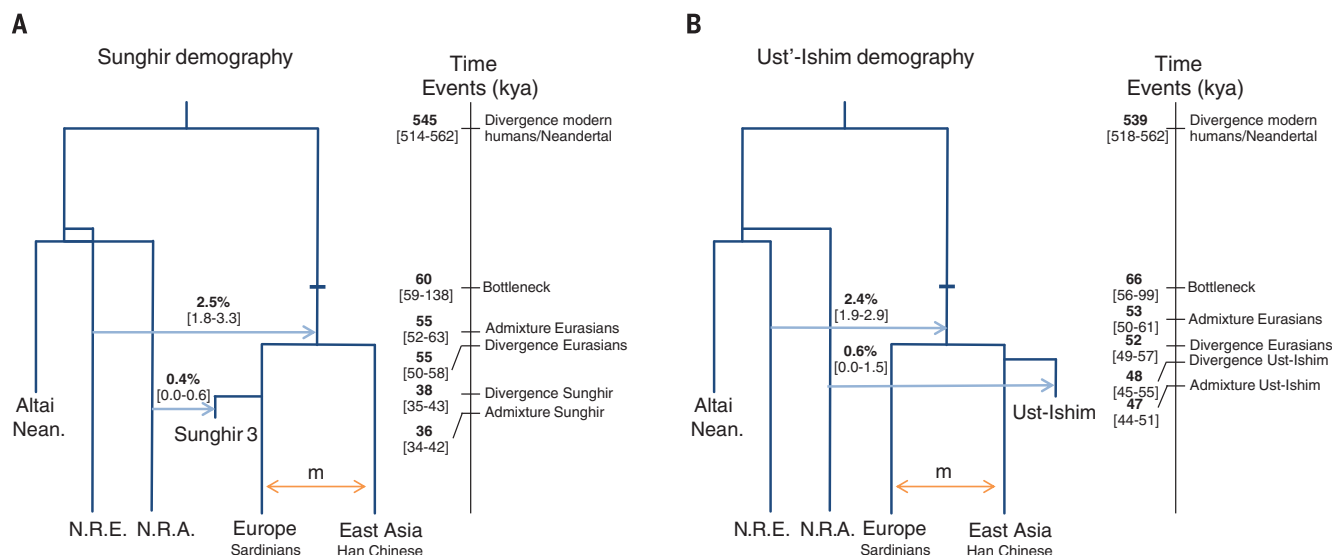


Fig. 4. Modeling of early Eurasian population history. (A and B) Best-fit demographic models for early Eurasian admixture including (A) SIII and (B) Ust'-Ishim. Point estimates are shown in bold (kya, thousands of years ago); 95% confidence intervals are shown within square brackets. Times of divergence in years are obtained assuming a generation time of 29 years and a mutation rate of 1.25×10^{-8} per generation per site. N.R.E.,

Unsampled "ghost" population related to the Altai Neandertal used to model admixture contributing to Eurasians; N.R.A., Altai Neandertal-related ghost population contributing to ancient modern humans. Divergence of SIII from proto-Europeans was supported in 100 of 100 bootstrap replicates, whereas divergence of Ust'-Ishim from proto-Asians was supported in 99 of 100 bootstrap replicates.

groups, leading to low genetic relatedness (20, 21). Some modern human groups exhibit increased levels of inbreeding, including populations where consanguineous marriage practices are encouraged, or geographically isolated HG groups such as those from the Amazon rainforest region (Fig. 2, A and C). In contrast, patterns of HBD among the Upper Paleolithic individuals are consistent with randomly mating populations of moderate effective size ($N_E \sim 200$), which suggests that close consanguineous mating was avoided (Fig. 2, A and C). Although our findings are currently limited to a single Upper Paleolithic site, if they are representative of early Upper Paleolithic HGs more generally, they reveal a social structure and cultural practices that emphasized exogamy. This is consistent with archaeological evidence of high mobility in the Upper Paleolithic (22), perhaps comparable to the scale of mobility seen ethnographically among small foraging bands at high latitudes (23). We note that this interpretation relies on the evidence that all individuals at Sunghir were contemporaneous and members of the same social group. This is clearly the case for the two children in the double burial (SII and SIII). It is possible that both SIV and SI were members of different social groups, potentially separated in time from SII and SIII. However, the shared material culture, overlapping radiocarbon date intervals, and close genetic relationship among all individuals support this inference.

Although the number of ancient genomes available remains small, the differences in inbreeding levels, and thus group organization, between AMH groups in the Upper Paleolithic and Neandertals are intriguing. The small reproductive groups of Upper Paleolithic AMHs at Sunghir apparently avoided inbreeding and its deleterious conse-

quences, in contrast to what has been observed for the Altai Neandertals. We caution that more genomic data on Neandertals from other regions is necessary to conclude whether the patterns observed in the Altai are representative of their genetic diversity more generally, or whether that individual was an outlier. Assuming the former, whether this would reflect ongoing extinction of Neandertals or a more general difference in social behavior and cultural practices also remains unknown. Our results nonetheless suggest that the human HG social structure of low levels of within-band relatedness, complex family residence patterns, relatively high individual mobility, and multilevel social networks were already in place among Upper Paleolithic societies 34,000 years ago. This social structure may have affected the development of cooperation and information transfer that underlie the evolution of culture in humans (20, 21, 24, 25) and may be crucial to understanding our species' unique evolutionary resilience and trajectory.

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ACKNOWLEDGMENTS

Supported by the FP7 Marie Curie program (CIG Nr 322261), Isaac Newton Trust, Leakey Foundation, and McDonald Grants and Awards Fund (P.R.N.); the H2020 Marie Skłodowska Curie program (EF Nr 656325) (M.D.B.); Swiss NSF grant 31003A-143393 (L.E., I.D., and V.C.S.); ERC Consolidator Grant 647787-LocalAdaptation (A. Manica); and the ERC's Seventh Framework Programme ("PalaeoChron" grant no. 324139) (T.H., T.D., and D.C.). GeoGenetics is supported by the Lundbeck Foundation, Danish National Research Foundation grant DNRF94, and the University of Copenhagen (KU2016 programme). We thank L. Moreau, M. Gerasimova, and A. Sinistyn for helpful discussions, and the staff of the Danish National High-Throughput DNA Sequencing Centre and the laboratory technicians of the Centre for GeoGenetics for technical assistance. Genomic data are available for download at the European Nucleotide Archive, accession number PRJEB22592.

SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/358/6363/659/suppl/DC1
Supplementary Text
Figs. S1 to S37
Tables S1 to S29
References (26–159)

22 June 2017; accepted 25 September 2017
Published online 5 October 2017
10.1126/science.aao1807

Ancient genomes show social and reproductive behavior of early Upper Paleolithic foragers

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Science **358** (6363), 659-662.
DOI: 10.1126/science.aao1807originally published online October 5, 2017

How early human groups were organized

Sequencing ancient hominid remains has provided insights into the relatedness between individuals. However, it is not clear whether ancient humans bred among close relatives, as is common in some modern human cultures. Sikora *et al.* report genome sequences from four early humans buried close together in western Russia about 34,000 years ago (see the Perspective by Bergström and Tyler-Smith). The individuals clustered together genetically and came from a population with a small effective size, but they were not very closely related. Thus, these people may represent a single social group that was part of a larger mating network, similar to contemporary hunter-gatherers. The lack of close inbreeding might help to explain the survival advantage of anatomically modern humans.

Science, this issue p. 659; see also p. 586

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